When the going gets tough, the tough get going: effect of extreme climate on an Antarctic seabird's life history

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Contents

1 Abstract

Individuals differ in many ways. Most produce few offspring; a handful produce many. Some die early; others live to old age. It is tempting to attribute these differences in outcomes to differences in individual traits, and thus in the demographic rates experienced. However, there is more to individual variation than meets the eye of the biologist. Even among individuals sharing identical traits, life history outcomes will vary due to individual stochasticity, i.e., to chance. Quantifying the contributions of heterogeneity and chance is essential to understanding natural variability. Inter-individual differences vary across environmental conditions. Heterogeneity and stochasticity depend on environmental conditions. We show that favorable conditions increase the contributions of individual stochasticity, and reduce the contributions of heterogeneity, to variance in demographic outcomes in a seabird population. The opposite is true under poor conditions. This result has important consequence for understanding the ecology and evolution of life history strategies.

2 Introduction

There exist two sources of variation in life history outcomes: *individual heterogeneity* and *individual stochasticity*. Individual heterogeneity refers to differences among individuals in life history traits that in turn affect the vital rates to which they are subject. Heterogeneity may be fixed or dynamic (reviewed by [1, 2]). Fixed individual heterogeneity may be due to e.g. genetic variation, epigenetics, maternal effects, or permanent environmental effects. Dynamic individual heterogeneity may be due to changeable factors such as age, experience, health, or dynamic environmental effects [3]. Individual stochasticity is variability in demographic outcomes that is generated by random events in the life cycle (surviving or not, reproducing or not, etc.). Individuals will differ in their life trajectories and demographic outcomes, even if they are subject to identical vital rates, because of chance alone [4, 5, 6, 7, 3, 8, 9, 10].

51   The relative importance of these sources of variation in life history outcomes is critically

52   important in improving our understanding of population dynamics and life history evolution,

53   and is currently a topic of intense debate [11, 10, 12, 13, 2, 8, 14]. Both theoretical models

54   and empirical studies have found that individual stochasticity contributes a large part of

55   the variance in life expectancy and lifetime reproduction, regardless of the variation of life

56   history traits and outcomes among individuals and regardless of life-history type (iteroparous

57   or semelparous) [14, 15].

58   Some individual differences are readily observable and easily incorporated as state vari-

59   ables (e.g., age, stage, size) in demographic models. Other differences are latent or un-

60   observed, variously referred to as frailty, latent heterogeneity, or individual quality (e.g.,

61   [16, 1, 17]). We refer to these as *unobserved heterogeneity*. Unobserved heterogeneity

62   can obscure, or even reverse, patterns of survival and reproduction at the individual level,

63   with consequences for population dynamics and our understanding of life history evolution

64   [18, 19, 20].

65   Environmental conditions affect the expression of heterogeneity. Harsh conditions may

66   remove frail individuals through physiological stress or increased resource competition. Harsh

67   conditions may also inhibit breeding, so that only robust or high-quality individuals survive

68   and breed successfully [21, 22, 23, 24]. Under favorable conditions, survival and breeding

69   may be high regardless of heterogeneity. Extreme climatic events may act as important

70   filters on the evolution of life histories [25, 26, 27].

71   The consequences of environmental conditions for life history outcomes such as life ex-

72   pectancy , lifetime reproduction, when unobserved heterogeneity is incorporated, are poorly

73   known and challenging to calculate. Our goal here is to partition the variance of several

74   life history outcomes between individual stochasticity and unobserved heterogeneity across

75   different environmental conditions.

76   The Southern fulmar (*Fulmarus glacialoides*), an Antarctic seabird, is the first wild

77   species for which the variance in life history outcomes was successfully partitioned into

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78 contributions from individual stochasticity and individual heterogeneity [19].

79 The Southern fulmar forages near the ice edge, which is an area of high productivity [28].
80 When sea ice concentrations are low, the distance from the colony to the ice edge is large and
81 foraging trips are longer. As a result, adults bring less food to their chicks, which then fledge
82 in poor body condition. This leads to reduced probabilities of breeding and breeding success
83 and reductions in population growth rate. Following [28], we define three environmental
84 conditions based on sea ice concentration: low, medium, and high (see Methods).

85 A capture-mark-recapture analysis including a latent heterogeneity variable revealed
86 three groups with distinct sets of life-history traits and outcomes that occur together [19].
87 We describe there groups below. The groups were estimated as fixed (at birth) heterogene-
88 ity; models with dynamic heterogeneity were not identifiable. Under medium environmental
89 conditions, heterogeneity explains only a small fraction of variance in life expectancy (5.9%)
90 and lifetime reproduction (22%). Here, we characterize how environmental conditions affect
91 unobserved heterogeneity in vital rates, life history outcomes, and growth rate in this popu-
92 lation. We estimate the relative contributions of individual stochasticity and heterogeneity
93 to variance in life history outcomes in the three environments.

94 3 Results

95 (a) Fulmar life history: heterogeneity and stochasticity

96 We estimated a stage-classified matrix population model (with the states pre-breeders,
97 successful breeders, failed breeders, and non-breeders); see Methods and [28, 19] for details.
98 We identified heterogeneity groups within the population by accounting for unobserved het-
99 erogeneity in CMR analysis. Three such life-history *complexes* (sets of life-history charac-
100 teristics that occur together through the lifetime of an individual [19]) exist, reminiscent of
101 the gradient of life-history strategy observed among species (i.e., the slow-fast continuum;
102 in birds: [29]; in mammals: [30, 31, 32, 33, 34]):

103   1. Complex 1 (14% of offspring at fledging) is a slow-paced life history where individuals

104   tend to delay recruitment, recruit successfully, and extend their reproductive lifespan.

105   2. Complex 2 (67% of offspring at fledging) consists of individuals that are less likely to

106   recruit, have high adult survival, and skip breeding often.

107   3. Complex 3 (19% of offspring at fledging) is a fast-paced life history where individuals

108   recruit early and attempt to breed often, but have a short lifespan.

109   "Quality" is a multidimensional property in this model. Individuals in complexes 1 and

110   3 are "high-quality" individuals [1] because they produce, on average, more offspring over

111   their lives than do individuals in complex 2. But complex 2 is made-up of individuals that

112   experience the highest levels of adult survival. Accordingly, we will compare the life history

113   complexes in terms of integrative demographic measures rather than abstract concepts like

114   quality or frailty. Finally, under medium environmental conditions, stochasticity explains a

115   large fraction of variance in life expectancy (94.1%) and lifetime reproduction (78%).

116   (b)   Environmental effects on life history heterogeneity

117   **Vital rates, individual differences and environments.**   To compare vital rates across

118   environmental conditions, we weighted the average vital rates by π, noted $\mathbf{E}_\pi(\theta)$. We found

119   that for all three life history complexes, breeding and success probabilities all decrease when

120   sea ice conditions are low, but adult survival remains unchanged (Fig. 1, Supplementary Ta-

121   ble 2). For example, the average breeding probability of previous successful breeder ($\mathbf{E}_\pi(\beta_2)$)

122   is 0.85 for medium sea ice conditions but declines to 0.56 when sea ice conditions are low.

123   The impact of sea ice conditions on vital rates depends on the complex individuals be-

124   long to (Fig. 1). For example, the breeding probability of previously successful breeders

125   (β_2) decreases by $\sim 17\%$ between medium and low sea ice conditions for complex 1 and 3

126   individuals, while it decreases by 45% for complex 2.

127   As a consequence, individual differences in vital rates depends on sea ice conditions. The

128   coefficient of variation over the mixing distribution π measures these individual differences

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129 in vital rates, standardized by the mean, and weighted by π (Methods). We found that

130 the difference in breeding and success probabilities among complexes increases when sea ice

131 conditions are low (Fig. 2). Differences between complexes are more pronounced for the

132 recruitment probabilities of pre-breeders, followed by the breeding probabilities of successful

133 breeders, the breeding success of pre-breeders, and that of successful breeders.

134 **Demographic outcomes, individual differences and environments.** In each envi-

135 ronment, the vital rates in each complex and the proportions of newborn individuals in

136 each complex define means and variances (among individuals) in eventual demographic out-

137 comes. We examine three integrative demographic outcomes: lifetime reproductive output,

138 life expectancy, and population growth rate λ. These quantities are calculated for each

139 environment, *as if* the population was living in such an environment permanently. This

140 counterfactual calculation is typical of population projections being used to characterize

141 the environment of a population by asking what would happen if that environment were

142 maintained permanently [35].

143 We calculate demographic outcomes using the population projection matrix $\mathbf{A}$ for λ

144 and the absorbing Markov chain implied by the matrix for calculating life expectancy and

145 lifetime reproduction (see Methods). State transitions defined by the vital rates (Fig 1)

146 and the time spent in each state (Fig. 4) interact to define life history outcomes (Fig. 3).

147 For example, life expectancy varies across environmental conditions even if adult survival

148 remains unchanged across sea ice conditions because adult survival differs among breeding

149 states and the transitions among breeding states depend on sea ice conditions. The average

150 life expectancy for complex 1 and 3 are larger for low sea ice conditions than for high sea ice

151 conditions (Fig. 3) because they spend most of their life as pre-breeder (i.e. 85% and 79%

152 of their lifetime, respectively; Fig. 4), a state that achieves higher levels of survival when

153 compared to adults (Supplementary Table 2).

154 Overall, mean demographic outcomes across complex vary among sea ice conditions. The

155 average life expectancy for the mixture of groups are larger for low sea ice conditions than

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156 for high sea ice conditions (red bars on Fig. 3). However, the average lifetime reproduction

157 is larger when sea ice conditions are high and smaller when sea ice conditions are low.

158 The impact of sea ice conditions on life history outcomes depends on the complex individ-

159 uals belong to. Individuals of complex 1 have the largest life expectancy, while individuals

160 of complex 2 experience the shortest for an environment characterized by medium or low

161 sea ice conditions (Fig. 3). In contrast, for high sea ice conditions, individuals of complex 2

162 achieve the highest life expectancy, while individuals of complex 3 experience the shortest.

163 In such high sea ice conditions, individuals spend most of their life as adult breeders, and

164 individuals of complex 2 have higher survival during adulthood than during the pre-breeding

165 stage, while individuals that belong to life history complex 3 have the lowest adult survival.

166 For an environment characterized by medium or low sea ice conditions, individuals in

167 complexes 1 and 3 produce, on average, more offspring over their lives than do individuals

168 in group 2 (Fig. 3). When sea ice conditions are low, individuals in complex 2 are unlikely

169 to recruit and their lifetime reproduction is null. However, for high sea ice conditions, indi-

170 viduals in complex 2 produce, on average, more offspring over their lives than do individuals

171 in complexes 1 and 3, because they experience a longer lifespan.

172 Finally, we calculated the population growth rate λ to integrate all the rates into a mea-

173 sure that shows how successful a set of vital rates in one environment would be. Individuals

174 of complex 3 have, on average, the highest λ regardless of environmental conditions (Fig 3).

175 ## (c)   Environmental effects on variance in demographic outcomes

176 The total variance in life history outcomes also varies across environmental conditions

177 (Table 1). The total variance of life expectancy is larger when sea ice conditions are extremely

178 low. On the other hand, the total variance of lifetime reproduction is much larger when sea

179 ice conditions are extremely high.

180 Both individual stochasticity and unobserved heterogeneity among individuals generate

181 variability in life history outcomes [5, 14], in response to changes in both within-group

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182 (stochasticity) and between-group (heterogeneity) variances. For example, both the between-

183 group and within-group variances of life expectancy increase when sea ice conditions are

184 extreme. However, for an environment characterized by high sea ice conditions the increase

185 in between-group variance is smaller than that in the within-group variance resulting in a

186 smaller proportion of individual heterogeneity to the total variance.

187 In spite of these complex patterns, the proportion of variance in life expectancy and

188 lifetime reproduction due to heterogeneity are smaller when sea ice conditions are high and

189 larger when sea ice conditions are low. Indeed, partitioning the variance in life expectancy

190 and lifetime reproduction reveals that only 2.7% of the variance in life expectancy and 0.4%

191 of the variance in lifetime reproduction are due to individual heterogeneity when sea ice

192 conditions are high, while 35.3% of the variance in life expectancy and 45.1% of the variance

193 in lifetime reproduction are attributable to heterogeneity when sea ice conditions are low

194 (Table 1).

4 Discussion

196 The impact of environmental conditions on unobserved heterogeneity in all fitness com-

197 ponents of a species has virtually never been studied. Three different life-history *complexes*

198 (sets of life-history traits that persist throughout the lifetime of an individual [19]) exist

199 within a population of Southern fulmar. Here, we show that the differences in vital rates

200 and demographic outcomes among complexes depend on the environmental conditions indi-

201 viduals experience. Importantly, differences across life history complexes are amplified when

202 environmental conditions get extreme. Sea ice conditions did not only affect patterns of

203 life history traits, but also the variance of life history outcomes and the relative proportion

204 of individual unobserved heterogeneity to the total variance. These novel results advance

205 the current debate on the relative importance heterogeneity (i.e. potentially adaptive) and

206 stochasticity (i.e. enhances genetic drift) play in shaping potentially neutral vs. adaptive

207 changes in life histories.

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208 Our results indicate that extreme sea ice conditions affect vital rates, and the difference
209 in vital rates among complexes depends on the environment fulmars live in (Fig. 1, 2).
210 In years when sea ice conditions were low, fulmars traveled greater distances to forage and
211 adults found less food to provision their chicks, ultimately affecting chick body condition and
212 fledging success [28]. Fulmars feed mainly on krill (*Euphausia superba*) and other crustaceans,
213 as well as on small fish (*Pleuragramma antarctica*) and squid [36]. During years with lower sea
214 ice conditions the abundance of preys, such as krill, may be reduced [37, 38]. As a result, the
215 breeding and success probabilities decline regardless of the complex individuals belong to, and
216 differences in vital rates among life history complexes are larger when sea ice conditions are
217 extremely low. Low sea ice conditions could intensify intra-competition for uneven resources
218 and reveal differences among individuals of different "quality" [24, 39, 40, 1, 41].

219 Differences among life history complexes in vital rates vary among reproductive states.
220 Individual differences in recruitment and success probabilities are larger for first-time breed-
221 ers than experienced breeding adults (Fig. 2), probably because of pre-breeders' limited
222 experience with foraging in their ability to acquire, store, and conserve energy resources
223 [42]. Individual differences in breeding and success probabilities are smaller for individuals
224 which previously failed or skipped breeding when compared to individuals that previously
225 succeeded. Raising an offspring successfully may impose an important energetic constraint
226 on the probability of breeding (successfully) the following year and may intensify differences
227 among complexes.

228 We also demonstrate that complexes differ in their demographic outcomes (life expectancy,
229 lifetime reproduction, population growth rate λ), which further depend on the environmen-
230 tal conditions experienced (Fig 3). Complex 1 individuals (slow-paced life histories, with a
231 delayed but high probability of recruitment and extended reproductive lifespan) have higher
232 life expectancy and lifetime reproduction than any other complex when sea ice conditions
233 are medium. Complex 2 individuals (low and delayed recruitment, skip breeding often, but
234 with highest adult survival rate) have higher life expectancy and lifetime reproduction than

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235 any other complex when sea ice conditions are high, but a null lifetime reproduction and

236 shortest life expectancy when sea ice conditions are low. Complex 3 individuals (fast-paced

237 life histories), have higher lifetime reproduction than any other life history complex when

238 sea ice conditions are low, and do achieve the lowest life expectancy in any environment.

239 Complex 3 individuals have the highest λ regardless of environmental conditions because

240 they breed at younger ages than any other complex across all sea ice conditions. For Southern

241 fulmars, recruitment probability is a key vital rate that has great potential in influencing

242 population growth rate [28]. Extreme low sea ice conditions select for robust and high

243 quality individuals (i.e complex 1 and 3 with $\lambda > 1$ Fig 3), because the competition for food

244 resources increases. Thus "*when the going gets tough, only the tough get going*". On the

245 other hand, when sea ice conditions are extreme high, all individuals are more likely to access

246 food ressources, hence survive and breed successfully, achieving a high fitness regardless of

247 the complex they belong to.

248 Finally, our results indicate that the variance of life history outcomes depend on envi-

249 ronmental conditions. The total variance in life expectancy are larger in extreme low sea

250 ice conditions, while the total variance in lifetime reproduction is larger in extreme high

251 sea ice conditions (Table 1). The total variance depends on the between and within groups

252 variances, which are function of the variances and means of the life history outcomes of each

253 group and the mixing distribution. The mean life expectancy of complex 1 and 3 are much

254 larger in extreme low than high sea ice conditions, which may contribute substantially to

255 the increasing total variance in life expectancy in low sea ice conditions. The mean lifetime

256 reproduction is much larger in extreme high than low sea ice conditions for complex 2, which

257 may contribute substantially to the increasing total variance in lifetime reproduction in high

258 sea ice conditions.

259 Partitioning this total variance in demographic outcomes reveals that 35.3 and 45.1%

260 of the variance in life expectancy and lifetime reproduction, respectively, is due to differ-

261 ences among complexes in a low sea ice condition, while only 5.9 and 22% of the variance

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262 is due to individual heterogeneity in a medium sea ice condition. This supports the hy-

263 pothesis that more variability in life history outcomes is attributable to persistent intrinsic

264 differences between individuals when competition intensifies for uneven resources [43, 24].

265 Indeed, differences across individuals in their ability to secure limited food resources may be

266 exacerbated when sea ice conditions are low [28], leading to the observed increased contri-

267 bution of individual heterogeneity to variance in life history outcomes.

268 In high sea ice conditions, 2.7 and 0.4% of the variance in life expectancy and lifetime

269 reproduction, respectively, is due to differences among complexes. In high sea ice conditions,

270 the foraging trips are shorter (sea-ice edge is closer to the colony) and food ressources likely

271 more abundant [28]. Hence, more variability in life expectancy and lifetime reproduction is

272 attributable to stochasticity under "favorable" conditions probably because all individuals

273 survive and breed successfully regardless of the complex they belong to.

274 Our results based on a deterministic analysis in each environment place bounds on the de-

275 gree to which individual heterogeneity can contribute to the variance of life history outcomes.

276 However, individuals experience diverses environmental conditions during their lifetime. A

277 stochastic model is required to partition the variance of life history outcomes between groups

278 and environmental conditions. Furthermore, individuals may belongs to various complexes

279 during their lifetime (i.e. dynamic individual heterogeneity). Unfortunately, a model to

280 estimate transitions among unobservable states is not identifiable [19]. Further work entails

281 exploring the consequences of such dynamic heterogeneity in a theoretical framework.

282 In conclusion, based on our findings in a long-lived vertebrate species, individual stochas-

283 ticity makes a substantial contribution to variance in demographic outcomes when environ-

284 mental conditions are favorable and medium, but individual heterogeneity contributes sub-

285 stantially to these outcomes when environmental conditions are poor. Because the strength

286 of selection on fitness components often varies considerably from year to year in wild popu-

287 lations [44], we expect phenotypic selection on hidden traits to intensify when conditions are

288 poor. These results advance the debate on how neutral versus potentially adaptive processes

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289 shape the variance of life history outcomes, and we further observe that the environmental

290 context is key in molding the relative contribution of these process to the evolution of life

291 histories. Finally, our findings support the hypothesis that both observed and unobserved

292 differences across individuals can be tempered by environmental conditions, and ultimately

293 define the diversity of life history strategies within a species.

5 Methods

Definition of environmental conditions Sea ice conditions affect the vital rates of Southern Fulmar [45], likely through their impact on food resources. In this population, individuals forage near the ice edge [28]. We use an index of sea ice condition which combines sea ice cover, and location of the sea ice edge (see [28] for more details on sea ice condition data and index calculation). We define low and high sea ice condition years as years with an index of sea ice conditions lower or higher than the 10th and 90th percentile of the sea ice condition distribution, respectively.

Estimating unobserved heterogeneity in vital rates To estimate both unobserved and observed sources of heterogeneity in vital rates, we use MultiState Mark-Recapture (MSMR) models with finite mixtures that account for imperfect detection [46, 47, 48] (Supplementary methods). Finite mixture MSMR models define a finite number of groups (hidden states) in the population and provide estimates for vital rates within each group. They also estimate the proportion of the sampled individuals falling into each heterogeneity group. We denote this distribution (the *mixing distribution*) $\boldsymbol{\pi}$. Mixture models have been intensively used in psychology, sociology, toxicology, and medicine to reveal the diversity of individual trajectories occurring within a population over time (see review in [48]). In ecology and evolution, few studies have used mixture models, and mainly for controlling for unobserved heterogeneity rather than trying to assess whether this heterogeneity influences within-population trajectories [48]. Here, we used these finite mixture MSMR models to reveal persistent life history complexes across contrasted environmental conditions.

We build on previous studies that identified 3 groups of individuals (i.e. life history complexes, [19]) based on unobserved heterogeneity in vital rates. We perform model selection to test for the effect of sea ice conditions on all vital rates of interest, once unobserved heterogeneity is accounted for. The best performing models selected (as measured by ΔAIC) comprised 90% of the overall AIC weight among the set of candidate models tested. The

320 model-averaged vital rates are shown in figure 1.

Coefficient of variation as a measure of differences among group   The coefficient of variation over the mixing distribution π is given by:

$$\mathbf{CV}_\pi(\theta_i) = \frac{\mathbf{SD}_\pi(\theta_i)}{\mathbf{E}_\pi(\theta_i)} \tag{1}$$

with θ_i a vector 3×1 of values for demographic rate i of the 3 groups of unobserved heterogeneity, for a specific environment. $\mathbf{E}_\pi(\theta_i)$ is the mean across unobserved heterogeneity group weighted by the mixing distribution: $\mathbf{E}_\pi(\theta_i) = \pi^\intercal \theta_i$ and $\mathbf{SD}_\pi(\theta_i)$ is the standard deviation calculated as:

$$\mathbf{SD}_\pi(\theta_i) = \sqrt{\mathbf{E}_\pi(\theta_i^2) - \mathbf{E}_\pi(\theta_i)^2} \tag{2}$$

321 **Life history outcomes and their variance**   We estimate life history outcomes (life ex-
322 pectancy, lifetime reproduction and age at first breeding) using absorbing finite-state Markov
323 chains [49, 4] for the three environments characterized respectively by low, medium, and high
324 sea ice conditions. We decompose the variance in life history outcomes into two components
325 — individual heterogeneity and individual stochasticity. Associated equations are detailed
326 for the Southern fulmar in an environment characterized by medium sea ice conditions in
327 [19].

328 **Growth rate**   We estimate individual fitness using a structured population model as the
329 growth rate of a group of individuals with the same realized life history [50]. Thus we
330 construct a population matrix for each complex (see supplementary material) and each set
331 of environmental conditions, and calculate the deterministic growth rate as the maximum
332 eigenvalue of this matrix [35].

Data accessibility

Datasets will be available via Dryad following publication.

Competing interests

We have no competing interests to report.

Acknowledgments

Funding

Authors' contributions

SJ and HC conceived the ideas, designed methodology and obtained funding for the analyses; CB and HW collected the data and obtained funding for field-work; SJ and SVD performed preliminary analyses; SJ analyzed the data; SJ led the writing of the manuscript with LA and HC. All authors interpreted the data, contributed critically to the intellectual content and gave final approval for publication.

356 Data accessibility

357   Data of this publication are archived at Dryad and available online at:

358 Tables

Table 1: Life expectancy and lifetime reproduction for the southern fulmar in three environments characterized by high, medium or low sea ice conditions. Results of the variance partitioning of demographic outcomes between individual stochasticity and unobserved heterogeneity are also shown. % H is the percentage explained by unobserved heterogeneity.

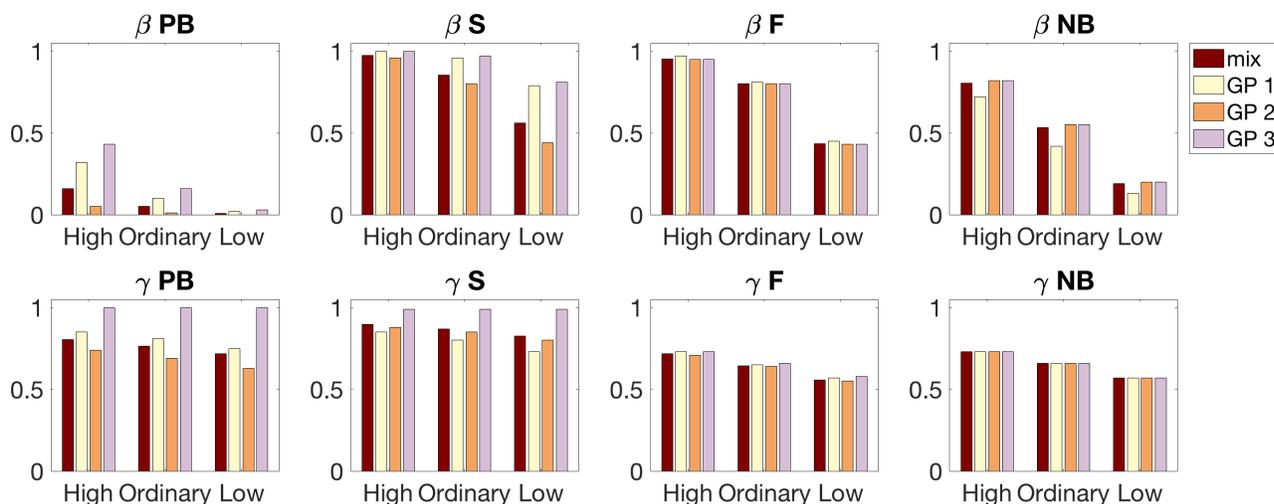|	Total variance	Within-group	Between-group	% Heterogeneity
HIGH				
Life expectancy	807.4	785.4	22	2.7
Lifetime reproduction	510.1	508.2	1.8	0.4
medium				
Life expectancy	200.4	188.7	11.7	5.9
Lifetime reproduction	55.7	43.5	12.3	22
LOW				
Life expectancy	1254.6	821.8	432.7	35.3
Lifetime reproduction	9.3	5.2	4.1	44.3

359 # figure

Figure 1: Vital rates of the southern fulmar for each reproductive state and sea ice conditions (SICs). Vital rates are averaged for environments characterized by: *high SICs* (1979, 1998, 2001), *low SICs* (1986, 1987, 2000) and *medium SICs* (all other years), as defined by [28]. Color bars refer to the 3 groups of unobserved heterogeneity (yellow: complex 1; orange: complex 2; and purple: complex 3), as well as the weighted average over the mixing distribution $\pi = [0.14\ 0.67\ 0.19]$ (maroon). The panels are ordered by reproductive state at the previous breeding season (column 1: pre-breeders (PB); column 2: successful breeders (S); column 3: failed breeders (F); and column 4: non-breeders) and vital rates (first line: breeding probabilities β; and second line: success probabilities γ). Note that survival probabilities do not vary with time nor sea ice conditions, and thus are not shown here but in electronic supplementary material.
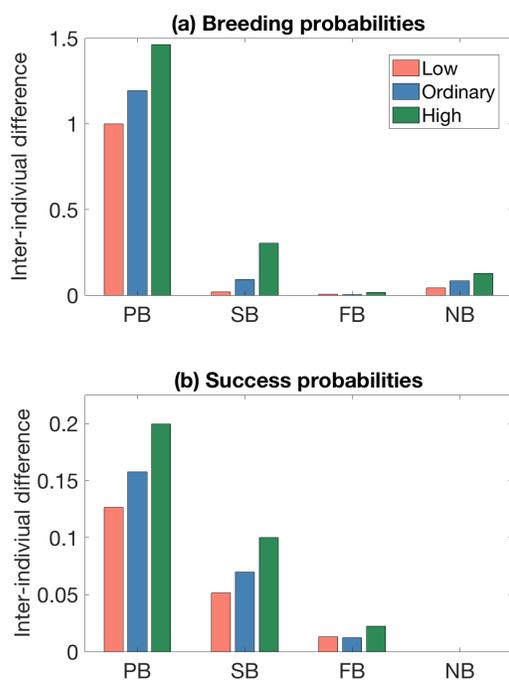
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Figure 2: Individual differences in (a) breeding probabilities and (b) success probabilities across life history complexes for each set of sea ice conditions (SICs). Inter-individual differences are measured by the coefficient of variation over the mixing distribution. The x-axis indicates the reproductive state (see figure 1 for legends) and the bar colors refer to SICs (low: red, medium: blue and high: green).
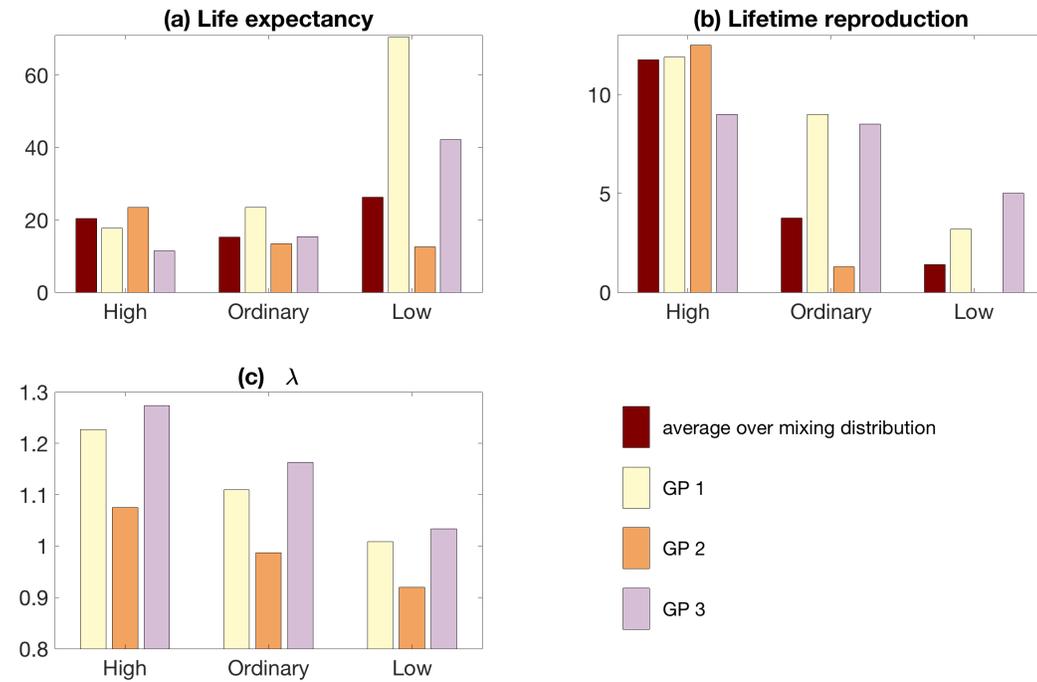
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Figure 3: Demographic outcomes of Southern fulmar for each complex for each set of sea ice conditions. Color bars refer to the 3 groups of unobserved heterogeneity (yellow: complex 1; orange: complex 2; and purple: complex 3), as well as the weighted average over the mixing distribution π (maroon).

(a) High SICs

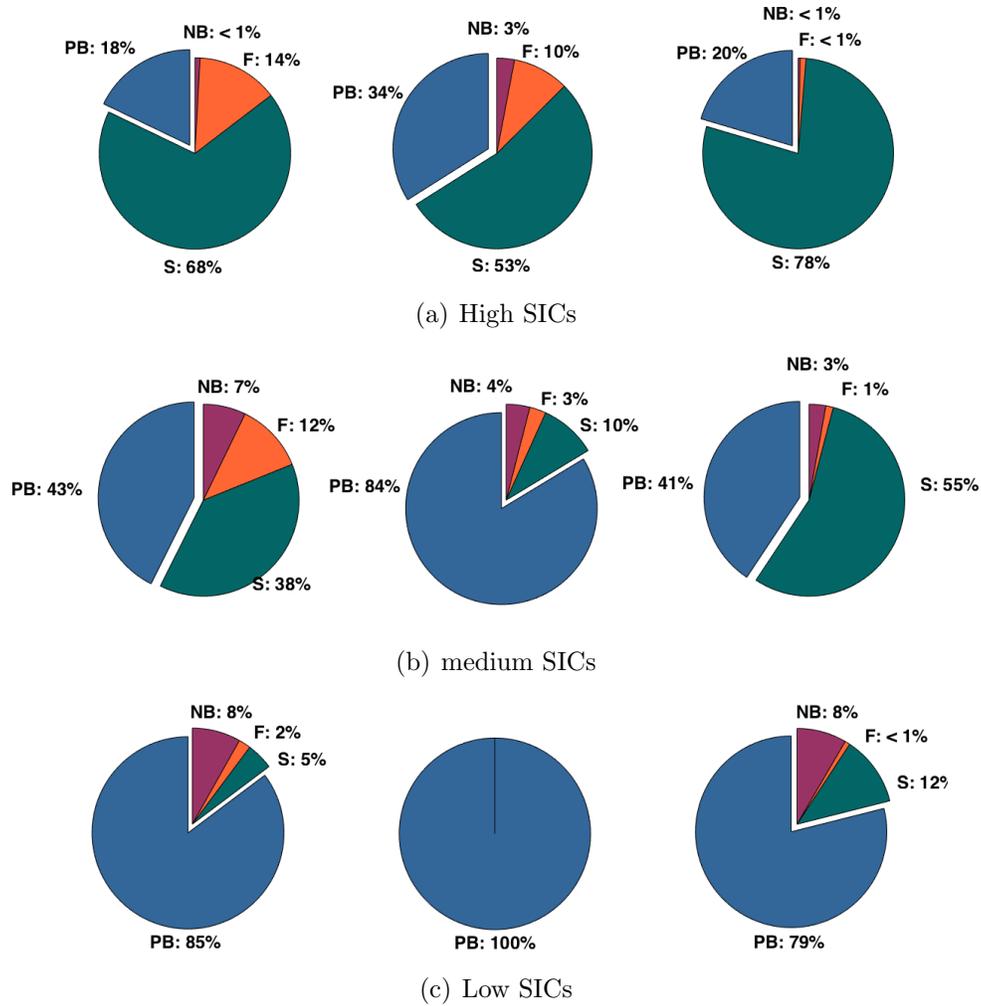
(b) medium SICs

(c) Low SICs

Figure 4: Percentages of time spent in each state for individuals in each complex for each set of sea ice conditions (a) high, (b) medium or (c) low. Complex 1 is shown by the left pie chart, while complex 3 is the right pie chart for each panel.

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